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The Social Ethology of the White Rhinoceros
Ceratotherium simum (Burchell 1817*)

By

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With 22 figures

Abstract

In a 3 ½ year field study the social system of the 2000 white rhinoceros in Umfolozi Game Reserve, Zululand, was investigated in a 30 km² area and four supplementary areas. Direct observation, individual recognition, tagging and attachment of radio transmitters gave copious information on spacing, grouping, movement, confrontation, territory occupation, rank order. Behaviour patterns are compared with those of the black and Indian rhinoceros, processes underlying their evolution are considered, weighing the influences of phylogeny, ecology, morphology, nutrition. Territorial structure was found to be a strong influence. Selective consequences for survival, reproductive success and progeny viability are discussed.

I. Introduction

Recent field studies on ungulates have revealed variations in social organizational patterns associated with the wide variety of habitats occupied by members of the included taxa (orders Proboscidea, Perissodactyla and Artiodactyla) (GEIST and WALTHER 1974). Attempts to account for this variability have placed differing emphasis on the importance of phylogeny, ecology, morphology and nutritional energetics (ESTES 1974, JARMAN 1974, GEIST 1974a). The rhinoceroses (Perissodactyla: Rhinocerotidae) are of special interest in potentially revealing the relative influence of these factors. As large herbivores, they share ecological similarities with the Proboscidea, Artiodactyla and Equidae. However, they have had an independent phylogenetic history probably since the Eocene (COLBERT 1969) and possess differing attributes in terms of body size, digestive physiology and weapons.

The white or square-lipped rhinoceros (*Ceratotherium simum*) is the most recent of the five extant species of rhinoceros (THENIUS and HOFER 1960), having apparently diverged from the African *Diceros* lineage during the course of the Pliocene (HOOIJER 1969). With adult ♂ ♂ reaching weights of about 2300 kg, it is today the third largest land mammal after the two elephants. In

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*) Dedicated to John T. EMLEN.

contrast to the browsing black rhinoceros (*Diceros bicornis*), the white rhinoceros is entirely a grazer, and is perhaps the largest purely grass feeding herbivore ever to have evolved. A southern population (*C. s. simum*) was historically widely distributed from Zululand northwards through the eastern and northern Transvaal to Rhodesia, Botswana and parts of South West Africa, inhabiting the drier forms of wooded grassland or "bushveld" (PLAYER and FEELY 1960, SIDNEY 1966). It was not recorded north of the Zambezi River, and thus was separated by a gap of some 2000 km from a northern population (*C. s. cottoni*), which occurred west of the upper Nile River in parts of Uganda, the Congo and Sudan. The subspecific distinction is based largely on a relatively minor difference in the outline of the dorsal concavity of the skull (HOOIJER 1969).

In association with the spread of firearms through southern Africa, the southern population declined to the brink of extinction between 1840 and 1895. The current population is derived entirely from a remnant of perhaps 100—200 individuals which survived between the Black and the White Umfolozi Rivers in Zululand. This area was proclaimed a game reserve in 1897, but protection did not become effective until 1920. Since then this population has increased steadily in numbers, and animals have been translocated to restock other parts of its former range. Despite the prior capture and removal of almost 1000 animals, the 1971 helicopter census recorded 2002 white rhinos remaining within the Umfolozi-Corridor-Hluhluwe game reserve complex. This population formed the basis of the present study.

Comparisons of the social systems of different species have been hampered by the use of subjective interpretive terminology by investigators in their initial descriptions. In particular, the terms "territory" and "dominance" have become somewhat ambiguous through the employment of varying definitions by different workers. In the following analysis, data will accordingly be presented initially in fundamental, objectively quantifiable terms, so far as is possible. Afterwards behavioural patterns will be interpreted conceptually and the selective processes responsible for their evolutionary appearance will be considered.

II. Methods

A. Study area

The Umfolozi-Corridor-Hluhluwe game reserve complex covers an area of 940 km² in Zululand, South Africa (28° 20′ S, 31° 50′ E). The region is characterised by hot, wet summers and a single winter dry season extending from May to late September. Annual precipitation averages 635 mm at Mpila Camp in Umfolozi Game Reserve and about 890 mm in Hluhluwe Game Reserve. Umfolozi Game Reserve consists mostly of gently undulating terrain at elevations of 50—300 m lying between the White and the Black Umfolozi Rivers. Higher hills chiefly along the western and southern boundaries rise to heights of 350—579 m. The predominant vegetation is an open woodland characterised by species of *Acacia* (with *A. tortilis*, *A. nilotica* and *A. nigrescens* most prominent). A well developed grass cover dominated by medium-tall *Themeda triandra* typifies much of the area, but over extensive sections short grassland including *Panicum coloratum*, *Urochloa mossambicensis*, *Digitaria argyrograpta* and *Sporobolus smutsii* occurs apparently as a result of heavy grazing pressure. Over much of Hluhluwe Game Reserve and the Corridor the country is hilly with open grassy slopes and small patches of coastal forest. Of the total white rhinoceros population of 2000, three quarters occurred within the 456 km² area of Umfolozi Game Reserve south of the Black Umfolozi River. Associated large herbivores include (minimum populations for the complex based on the 1970 helicopter census are in brackets) impala *Aepyceros melampus* (8235), wildebeest *Connochaetes taurinus* (6363), nyala *Tragelaphus angasi* (3845), warthog *Phacochoerus aethiopicus* (3123), zebra *Equus burchelli* (2744), buffalo *Syncerus caffer* (1717), waterbuck *Kobus elypsiprimnus* (1335), kudu *Tragelaphus strepsiceros* (1118), black rhinoceros

Diceros bicornis (300) and others. The overall large herbivore biomass exceeded 63,7 kg/ha. Lions (*Panthera leo*) reappeared in the area in 1958, cheetahs (*Acinonyx jubatus*) have been reintroduced, and leopards (*Panthera pardus*) and hyenas (*Crocuta crocuta*) have persisted.

Intensive observations were conducted in a 30 km² area around the Madlozi game guard outpost in the western section of Umfolozi Game Reserve. Comparative data were obtained from four supplementary study areas elsewhere in the Complex. White rhino population density in the Madlozi study area averaged 5.3 animals per km², and this seemed typical of much of the western section of Umfolozi Game Reserve.

B. Techniques

Field work was carried out between January and July 1966, and then from November 1968 to September 1971. The study period thus covered 3½ years, but encompassed an overall time span of 5¾ years. About 2500—3000 hours were spent in direct observation of white rhinos (including 75 hours at night over full moon periods). Observations were made mostly on foot, facilitated by the poor visual acuity of the subjects, which did not detect a stationary person at ranges over about 30 m. This allowed great freedom in following the movements of the animals, which usually remained unaware of the presence of the observer. Patrols were of two types, either transecting an area, recording the numbers, locations, activities and identities of all rhinos encountered; or selecting one particular individual or group and maintaining it under continuous observation for several hours. All adults and many immature animals could be distinguished individually, using mainly variations in horn sizes and shapes (photographically documented). 45 individuals, mainly subadults, were marked with coloured eartags, and 10 individuals (seven cows, two subadult ♂ ♂ and one beta adult ♂) were equipped with radio transmitters for telemetric monitoring of movements (OWEN-SMITH 1972). In the Madlozi area 314 different individuals were identified, of which 135 familiar individuals could be recognized instantly on sight. A further 363 individuals were distinguished in other study areas. Spatial locations were plotted on 1 : 18 000 topographic maps with estimated accuracy usually within ± 50 m.

III. Results

A. Ecological background

The white rhinoceros is entirely a grazer, using its broad lips to pluck grass generally 2—5 cm above soil level (OWEN-SMITH 1973). At Umfolozi, areas of short grass grassland were favoured grazing locations for much of the year, and white rhino grazing pressure was probably an important factor maintaining these grasslands. The grasses growing in such areas comprised mainly stoloniferous and leafy species, which contain less fibre and hence are relatively more nutritious. During the later dry season, when short grass areas had beed cropped close to ground level and were no longer productive, feeding was transferred to remaining stands of tall grass dominated by *Themeda triandra*. Though this dry grass is probably submaintenance in protein levels (THORNTON 1968), few animals showed any notable loss in body condition during this period. Their large body size and correspondingly low metabolic rate per unit of body tissue probably buffers them against excessive weight loss during the winter starvation period (BELL 1971).

Main feeding periods occurred during the early morning and early evening, but grazing continued in spells through the night. During cloudy or mild weather animals could be active at all times of day, but on hot, sunny days, particularly in summer, they rested lying or standing for 5—8 hours through the midday period. Certain shady localities situated on low ridgecrests were favoured for this purpose, and sometimes 20—30 rhinos congregated in such rest-place areas. Wallowing in water or mud sometimes took place around midday, but also occurred at other times of the day or night.

In summer water is plentifully dispersed in numerous small pools lying in depressions or "pans" and along drainage lines. Under such conditions, animals drank once or twice daily. As the dry season progressed, water sources became increasingly restricted. Perennial supplies were available only from the two Umfolozi Rivers and from two or three small springs, though a few long-lasting pools retained water for much of the dry season. However, no part of the reserve was more than 8 km away from one of the rivers. During the late dry season, many animals had to undertake special journeys to water at intervals of 2 and 4 days. The journey was usually made during the early evening, and animals usually followed one of the network of trails which converged on watering points.

No instances of predation by lions or other carnivores were recorded during the study period (though two cases of white rhinos killed by lions have subsequently been noted: HITCHINS (pers. com.) and PIENAAR (1970) records an unsuccessful attack by lions on an adult bull in the Kruger Park). I watched lions in the close proximity of white rhinos on three occasions, but the white rhinos seemed unconcerned and the lions disinterested.

B. Social structure

1. Social categories

Five social categories differing in their patterns of interaction, spatial dispersion and roles in reproduction were distinguished: (i) juveniles (juv.); (ii) subadults (sa); (iii) cows (AD♀♀); (iv) alpha ♂♂ (α♂♂); (v) beta ♂♂ (β♂♂). These are basically age/sex classes, except for the distinction between two categories of adult ♂.

Juveniles were driven away by their mothers, upon the birth of a subsequent calf, at 2—3 years of age, and were thereafter regarded as subadults. Some authors (for example WALTHER 1972a) have differentiated prepubertal from post- pubertal immatures, terming the former "adolescents". This distinction will not be followed here, as there were no easily discernible field criteria to indicate the attainment of physiological sexual maturity. Young ♀♀ underwent their first oestrus at about 5 years of age, but remained in subadult groups until the birth of their first calf at 6.5—7 years of age. Thereafter they were usually accompanied only by the offspring and were regarded as cows. Some subadult ♂♂ became solitary at about 8 years of age, but still tended to attach themselves temporarily to cows or other subadults until 9—10 years of age. Others remained paired up with a similarly aged companion until 11—12 years of age, by which time they became virtually indistinguishable in appearance from fully mature ♂♂, except by the less worn appearance of their horns. Young ♂♂ were regarded as adult once they became solitary between 10 and 12 years of age and assumed either α♂ or β♂ behaviour patterns.

About one third of all adult ♂♂ were β♂♂. Though there was no distinct age separation, the category of β♂ included a higher proportion of individuals judged to be either young or old (based on the degree of development or wear of the horns; Table 1).

Table 1: Age distribution of α♂♂ and β♂♂

	No. of indiv. classified	young adults	prime adults	old adults
α ♂♂	36	3	30	3
β ♂♂	23	7	7	9

2. Groupings

White rhinos were encountered singly and in clusters of varying size and cohesion. Some clusters were evidently merely the result of several individuals congregating in a favourable grazing area or at a rest-place. Such *aggregations* separated into smaller units with time as the constituent animals followed independent paths of movement. However, in other associations individuals orientated to one another's movements so as to remain in proximity. An association of one or more individuals exhibiting such cohesive tendencies will be

Fig. 1: Groupings. For a l l g r o u p s, N = 1432 groups, about ³/₄ of these in the Madlozi area. For s t a b l e a s s o c i a t i o n s (groupings persisting intact in sightings spanning one month or longer), N = 935 monthly recorded based almost exclusively on the Madlozi area. Figures represent percentage of individuals that were associated with companions of each social category in each group size class. Lines clarify successive additions in building up larger groups

(a) Cows

(i) All groups
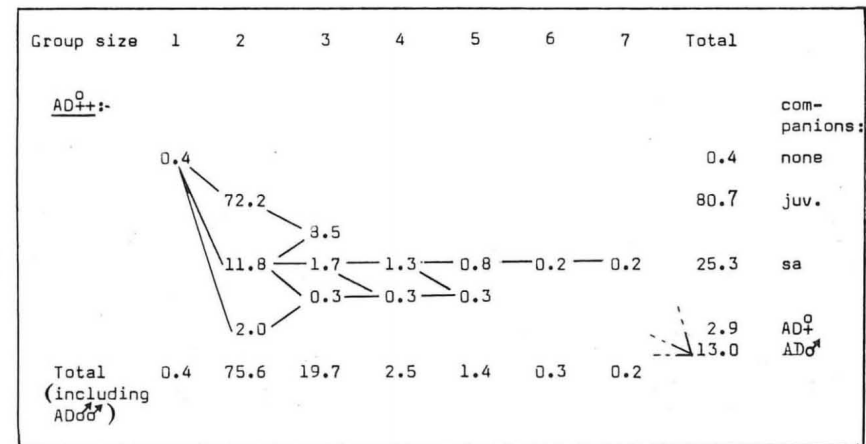
(ii) Stable associations
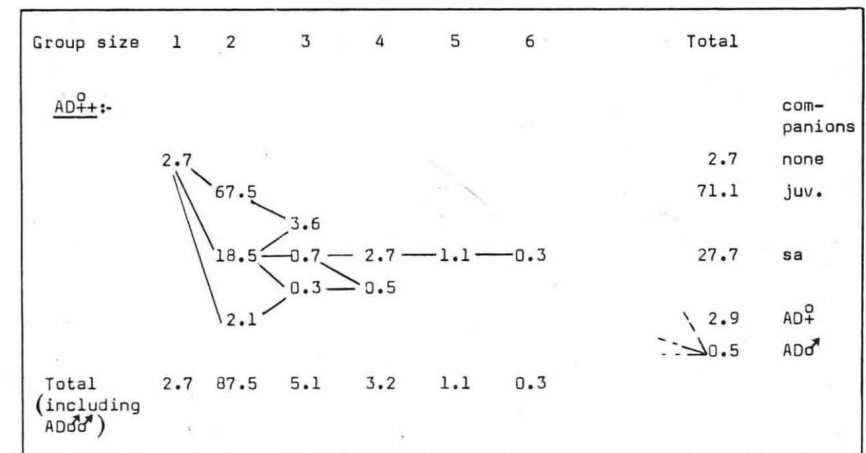
termed a *group*. Groups may be differentiated further by the duration of the association between member individuals. All groups remained intact for at least several hours. Groupings in which the same individuals were seen together over a period of one month or longer will be termed *stable associations*. Groupings cohering for shorter periods will be termed *temporary associations*.

About ³/₄ of adult ♀♀ were accompanied only by a single juvenile offspring (Fig. 1[a]; the lower percentage recorded for stable associations can be ascribed merely to the capture and removal of some juveniles from the Madlozi Area). Cows without a juvenile companion were usually accompanied by one, or occasionally by up to six subadults. Sometimes a subadult was found with a mother-offspring pair, but most of such associations were temporary, the sub-adult remaining with a particular cow and calf for a few days only. In some cases the past history of a subadult showed it was definately not an offspring of the cow it was accompanying. Nevertheless, associations between particular cows and subadults frequently persisted for several months or even years, usually being terminated only by the birth of a new calf to the cow. For cow-sa ♂ pairs the average minimum bond duration, based on the interval between the first and last recorded sightings of a stable association, was 8.1 months (max. 22 months, N = 8); while for cow-sa ♀ pairs this was 10.3 months (max. 26 months, N = 12). Some 2.9 % of cows were accompanied by a second adult ♀

(b) Adult ♂♂

(i) All groups
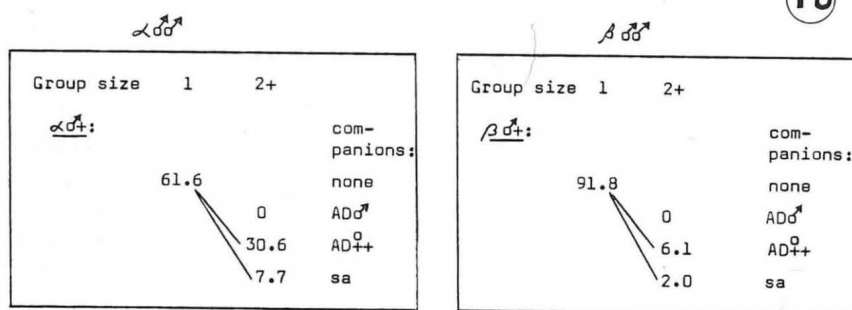
(ii) Stable associations
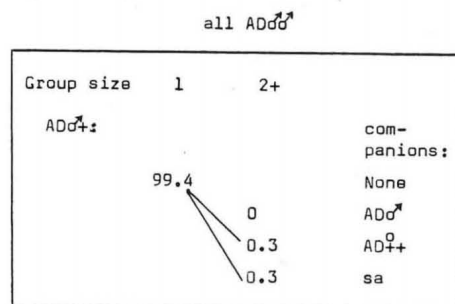
(c) Subadults

(i) All groups
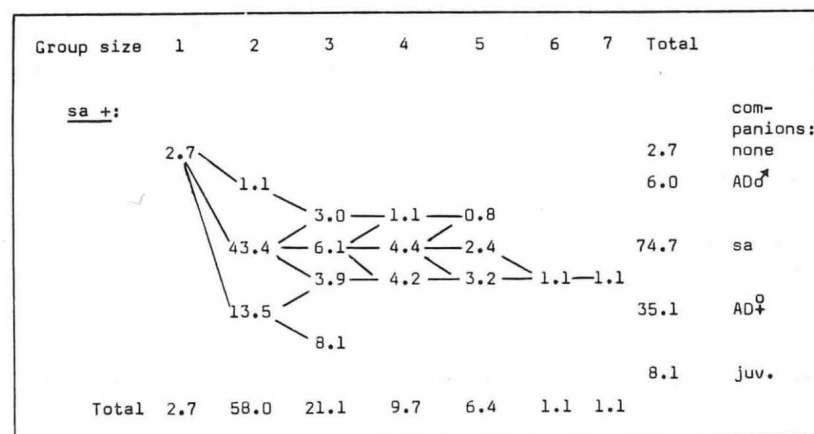
(ii) Stable associations
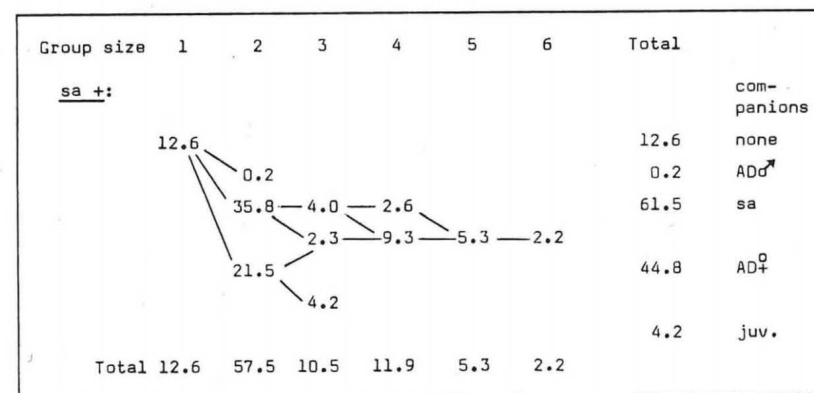
(sometimes with the additional company of one or more subadults). One pair of adult ♀♀ remained together for the full five months of the 1966 study period, while another two cows were always found together over a four month period, until one of them gave birth. In the latter case both cows appeared of similar age, and a mother-offspring relationship could be discounted. Some 13 % of cows were additionally accompanied by a single adult ♂, but such associations rarely persisted longer than 2—3 weeks. Solitary cows were exceptional.

Adult ♂♂ were basically solitary except for temporary periods of attachment to cows or to sa ♀♀ (Fig. 1 [b]). However, while α♂♂ were recorded accompanying a cow or sa♀ in 38.8 % of sightings (N=345), β♂♂ were associated with a ♀ in only 8.1 % of sightings (N = 114). Also, associations between a β♂ and a cow rarely lasted longer than a day, while α♂♂ frequently attached themselves to particular cows for periods of 1—2 weeks. Associations between an adult ♂ of unknown status and a sa ♂ were seen twice, but not in the study areas.

Most subadults not accompanying cows were associated with a similar aged companion of the same or opposite sex (Fig. 1 [c]). Subadult groups numbering up to five individuals were recorded, but associations of more than two individuals tended to be unstable. For sa♂-sa♂ pairs, an average minimum bond duration of 11.3 months was recorded (max. 26 months, N = 13); for sa♀-sa♀ pairs 3.7 months (max. 9.5 months, N = 14), and for sa♂-sa♀ pairs 4.2 months (max. 15.5 months, N = 13); but results are distorted on the low side both by rhino capture operations and by dispersal movements.

3. Intra- and intergroup spacing

Group companions maintained interindividual distances usually less than 5 m (one body length) during periods of active feeding, and were seldom separated by more than 20 m (5 body lengths). (Table 2). Subadults that were only temporarily attached to a particular cow maintained greater spacings than sub-

Table 2: Intra-group spacing during feeding. Spacing recorded at 5 min intervals

Group type	aver.	range	max. rec.*	Distribution 0 - 4	5 - 9	10 - 19	20 +	N
1. AD♀ + juv.	2.7	0.2 - 25	25	.86	.10	.03	.01	200
2. AD♀ + sa	5.7	1 - 25	45	.58	.23	.16	.03	131
3. AD♀ + sev. sa								
(i). from AD♀	11.2	1 - 40	40	.33	.18	.33	.18	61
(ii). AD♀ from nearest neighb.	2.3	0.5 - 6	6	.92	.08	0	0	13
(iii). sa from nearest neighb.	3.7	1 - 14	14	.77	.16	.07	0	61
4. AD♀ + AD♀	8.1	1 - 35	35	.36	.33	.25	.06	64
5. sa + sa	2.9	0.5 - 11	11	.77	.18	.05	0	40
6. temp. sa								
(i). from AD♀	10.5	1 - 40	150	.25	.30	.29	.15	264
(ii.) from nearest neighbour	6.2	1 - 40	40	.44	.32	.20	0	257
7. AD♀ + AD♂	15.0	3 - 60	sev. 100	.02	.19	.60	.19	118

* Including observations outside sampling regime.

adults that were bonded in a stable association. Adult ♂♂ accompanying cows usually kept 2—5 body lengths away, and were only rarely tolerated within one body length.

While resting, interindividual distances were reduced, and animals commonly lay almost touching (Table 3).

Table 3: Intra-group spacing during resting

Group type	Interindividual distances (m) mean	range	N
AD♀ + juv.	0.5	0 - 1	6
AD♀ + sa	0.7	0.2 - 2	12
AD♀ + cow	0.8	0.5 - 2	4
sa + sa	2.2	0.5 - 4	8
Temporary sa from nearest neighbour	3.6	0.5 - 15	10
AD♀ + AD♂	9.7	2 - 20	13

The extended visibility prevailing over a formerly bush-cleared zone at Madlozi permitted mapping of the positions of a number of adjacent groups without bias. Nearest neighbour analysis (following CLARK and EVANS 1954) of intergroup spacing among grazing animals revealed a significant tendency towards aggregation by rhino groups in general (Table 4). Since some degree of

Table 4: Analysis of inter-group spacing (following CLARK and EVANS 1954). Based on mapped dispersions of grazing rhinos in the Madlozi bush-cleared zone. Estimated mean rhino density = 6.4/km²; mean group density = 3.3/km²

(a) All groups considered	α♂	β♂	AD♀ +	sa
Mean distance to nearest neighbouring group r_a (m)	227	224	147	125
expected r_e in random distr (m)	276	276	276	276
ratio r_a / r_e	0.82	0.81	0.53	0.45
Sample size N	42	39	178	24
s (r_e)	23.3	24.1	10.78	29.3
Standard normal variate z	2.10	2.16	12.0	5.15
signif. of difference from random	p < 0.05	p < 0.05	p < 0.01	p < 0.01

(b) Only groups of same type considered	α♂ / α♂	β♂ / α♂	β♂ / β♂	AD♀ / AD♀
Estimated mean density / km²	0.62	1.25	1.25	2.15
Mean nearest neighbour distance r_a (m)	891	406	409	195
expectet r_e if random	635	447	447	342
r_a / r_e	1.40	0.91	0.91	0.57
Sample size N	48	75	28	168
s (r_e)	48.0	36.0	62.7	13.8
standard normal variate z	5.33	1.14	0.61	10.7
signif. of difference from random	p < 0.01	n. s.	n. s.	p < 0.01

contagion was probably due to patchiness in the most favourable grazing locations at any one time, interest lies especially in the differences between the patterns for different social categories. If particular group types are considered separately (for example, measuring distances from cow groups to the nearest neighbouring *cow* group), cow groups still show strong aggregative tendencies with respect to one another. In contrast, a♂♂ exhibit a tendency towards a uniform distribution with respect to other a♂♂; while the distribution of β♂♂ with respect to either nearest a♂ or nearest β♂ is not significantly different from random (in the latter case, only a♂♂ and β♂♂ coinhabiting the same area were considered; see next section).

Distributions observed during midday resting periods were highly clustered, since different groups commonly resorted to the same resting areas. Here they lay spaced either a few metres apart in the shade of the same trees, or 10—15 m separate under adjacent trees.

4. Spatial utilization patterns

(i) Cows. Each individual showed a favoured area of occupancy, the limits of which varied depending upon prevailing conditions (Fig. 2). Cows moved over a wider area when forage quality was deteriorating than when green grass was plentifully available, irrespective of season. When water was unavailable within this area, outlying sightings were recorded which could be related to journeys to and from nearby water sources.

Table 5: Home range sizes of cows.
Areas measured planimetrically after connecting outlying points
The home ranges of cows P and O are those mapped in Figure 2.

Individual	observ. period (mo.)	points of location		Areas (km²)		
		radio-telem.	total	core area	home range	annual range
P	30	110	158	5.7	11.4	18.2
O	33	89	173	5.3	9.1	19.6
U	37	87	203	7.9	14.7	16.1
V	12	42	72	5.3	13.6	16.2
AL	5	57	62	6.3	10.2	14.7
ZZ	22	42	54	7.4	10.9	20.5
J	37	0	114	9.6	14.0	15.3
AA	31	0	100	6.4	8.9	8.9
Mean				6.7	11.6	16.2

When grass was green and water abundant, there was no incentive for individuals to move beyond their most favoured localities; the area occupied under such conditions will be referred to as the *home range core area*. The area utilized under all forage conditions while water was still readily available will be termed the *home range*. The total area including excursions to and from outlying water sources will be termed the *annual range*. The added peripheral area was not utilized while water was available within the home range, and animals usually returned to within the home range between such waterhole visits. (See JEWELL 1966 for a discussion of these terms).

The spatial areas encompassed by connecting outlying points were measured planimetrically for the eight best-known cows, yielding the following means (Table 5): home range — 11.6 km² (range 8.9—14.7 km²); core area — 6.7 km² (range 5.3—9.6 km²); annual range — 16.2 km² (range 8.9—20.5 km²). These estimates are to be regarded as minimal, particularly that referring to the annual range. Some cows apparently moved away briefly at the end of the

dry season to the vicinity of one of the rivers, where they were beyond radio-telemetric range (except in one instance for the cow O, see Fig. 2). Cows having a perennial water supply within their usual home area did not wander so widely (for example the cow AA in Table 5).

The home range core areas of individual cows overlapped extensively with one another (Fig. 3), and all sections of favourable habitat were utilized by numerous different individuals.

Fig. 3: Overlay of home range core areas for 25 cows regularly frequenting the Madlozi study area. Lines connect outlying points of location for each individual under conditions of abundant water and green grass

There was no indication of any division among cows into discrete "home range groups" (HUNTER 1964) or "clans" (KURT 1968). Each seemed to move over her own individually distinctive home range independently of the movements of others.

(ii) Alpha ♂♂. In contrast points of location for individual α♂♂ were clustered within discrete mutually exclusive areas (Fig. 4). These *territories* formed a contiguous mosaic with no unoccupied areas except for steep hillsides (Fig. 5). Territory size based on all study areas averaged 1.65 km² (range 0.75—2.60 km²,

Fig. 2: Points of location for two cows, Madlozi study area, Dec. 1968—Sep. 1971. Up to three points per day (early morning, midday, late afternoon) have been plotted

Table 6: Territory sizes

study area	popul. dens / km²	total extent km²	no. of territ.	territory size	
				mean km²	range
Madlozi , 1966	5.3	6.5	4	1.62	0.75 - 2.2
Madlozi , 1971	5.3	19.7	11	1.79	1.2 - 2.6
Nqutsheni	7.0	5.1	5	1.02	-
Gqoyini	5.1	7.5	4	1.88	-
Dengezi	ca. 2.5	6.1 +	3	2.03 +	-
All		44.9	27	1.65	0.75 - 2.6

Legend for Fig. 2:
- WATER ABUNDANT, GRASS GREEN
- WATER IN SEVERAL LOCATIONS, GRASS DRYING
- WATER RESTRICTED TO FEW LOCATIONS, GRASS BROWN
- RADIO-TELEMETRIC LOCATIONS
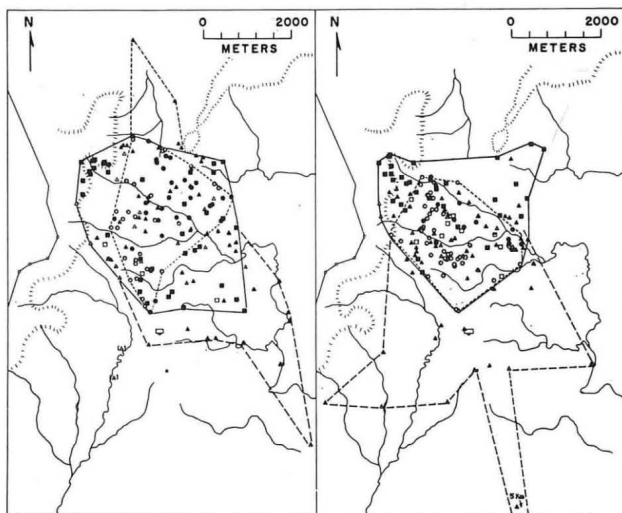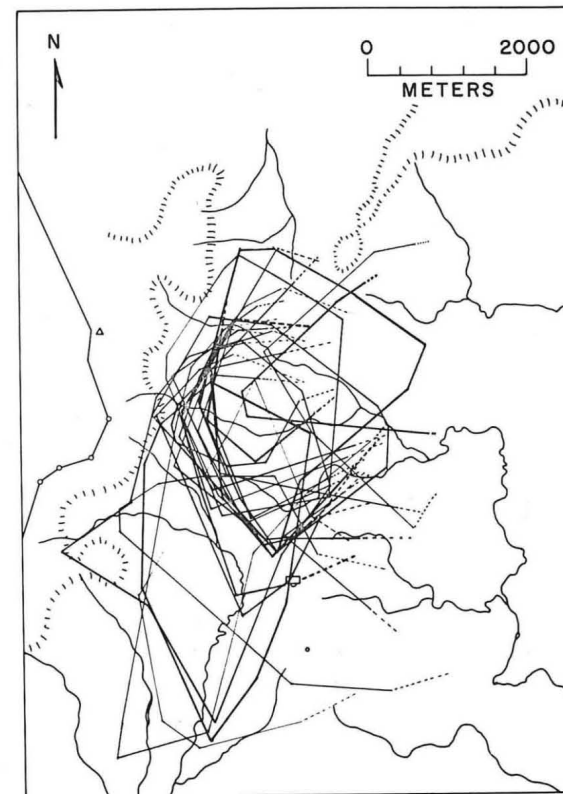- .... HOME RANGE CORE
- —— BASIC HOME RANGE
- – – – ANNUAL RANGE

INDIVIDUAL

| NO. LOCATION RECORDS | □ 74 | ● 114 | ▽ 70 | △ 34 | ○ 78 | ■ 34 |

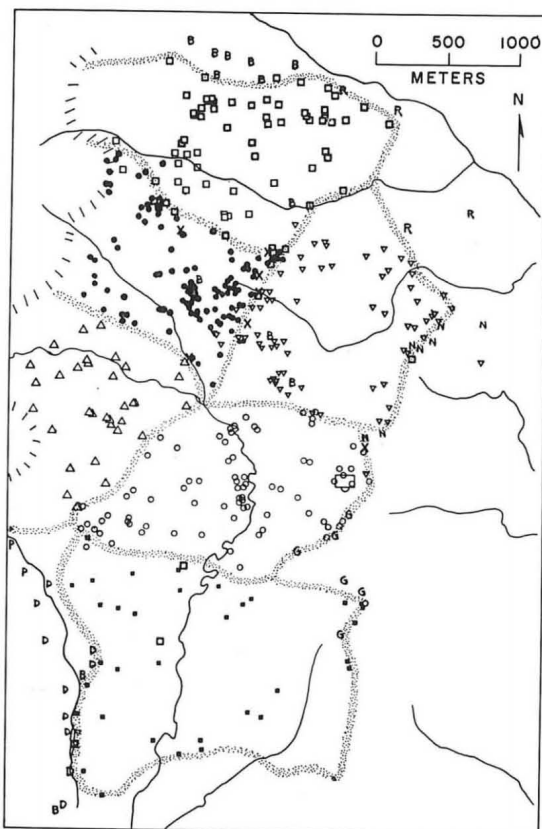X = LOCATION OF CONFRONTATIONS BETWEEN ♂'s

▓▓▓▓ TERRITORY BOUNDARIES

Fig. 4: Points of location for six α ♂♂, Madlozi study area, 1 June 1970 — 4 Sept. 1971. All brief sightings of each individual have been plotted, plus first and last locations on each day that individuals were kept under constant observation. Additional locations have been included where these are of significance in relation to boundaries. The period is one during which no changes in territory occupation occurred. Letters indicate adjacent sighting locations of other α ♂♂. (N o t e : a perennial spring is located in the lower left hand corner of the map)

lineate limits. By noting the number of changes in occupancy in relation to the total period for which each territory was observed (Table 7), the average duration of occupation of the same territory by an individual α♂ is estimated to be 5.4 years.

Territory boundaries only sometimes coincided with physical features such as watercourses or ridgecrests. They were revealed by a sharp transition in the relative likelihood of encountering either of two neighbouring α♂♂ (Fig. 6),

Table 7: Changes in territory ownership occurring during the study period

STUDY area	no. of territ. observed	no. of changes	sum of observ. durations* (yrs)
Madlozi	15	11	49.5
Nqutsheni	6	0	9.3
Gqoyini	4	0	3.2
Dengezi	4	1	3.3
All	29	12	65.3

* Sum of the periods between the first and the last sightings of the alpha ♂ in each territory.

Fig. 5: The territory mosaic, Madlozi study area, as of June 1971
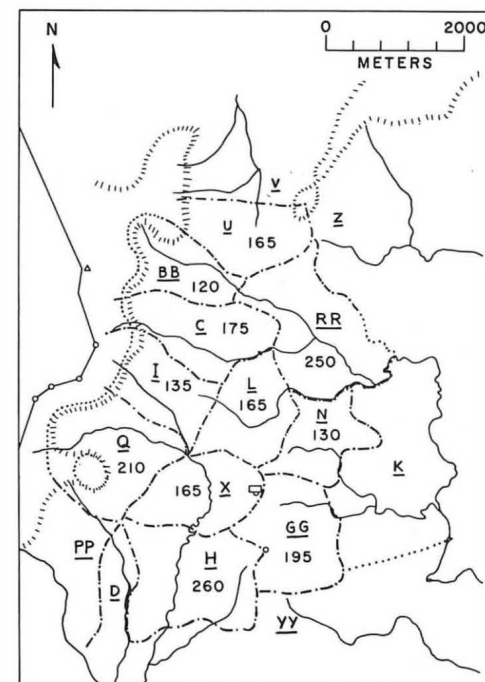
—·—·— TERRITORY BOUNDARIES

············ (TENTATIVE)

LETTERS = INDIVIDUAL TERRITORY HOLDERS

FIGURES = TERRITORY EXTENT IN HECTARES

and by certain behavioural actions which tended to occur at boundaries. Alpha ♂♂ frequently patrolled along boundary regions (Fig. 7), spray-urinating repeatedly while doing so; engaged in occasional confrontations with neighbours at borders (see Fig. 4) and blocked the progress of oestrous cows in the vicinity of boundaries (Fig. 8). Occasionally α♂♂ proceeded as far as 100 m across a putative boundary "line", but more usually they veered quietly aside upon coming into the boundary region. Boundaries can be regarded as narrow "tension zones" perhaps 50—100 m wide where the ranges patrolled by two neighbouring α♂♂ overlapped; however α♂♂ grazed more usually 100—200 m on their own side of the boundary than in the actual boundary region.

All territories contained sections of both tall and short grass grassland and seemed adequate to supply the year-round food requirements of the resident α♂. One or two midday resting sites were included as well as one or more temporary pools for drinking and wallowing. Alpha ♂♂ rarely wandered outside their own territory limits, except during the late dry season when many became forced to make excursions to and from water every 3—4 days. The frequency with which α♂♂ were recorded more than 100 m beyond their putative territory boundaries was only 0.6 % (N = 870) under wet season conditions, but increased to
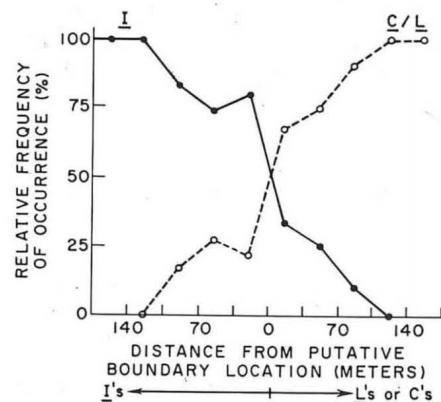
Fig. 6: Relative frequencies of occurrence of neighbouring α ♂♂ across a boundary zone. Determined by counting points of location in successive 35 m wide strips parallel to putative boundary lines (N = 191 points)

Fig. 7: Daylight movements of α ♂ I over three consecutive days, 30 Mar.—1 Apr. 1971

— GRAZING
→ WALKING
▲ MIDDAY REST
△ OTHER RESTS
○ DEFECATION
+++ URINATION
░░░ TERRITORY BORDER

N
0   1000
METERS

6.9 % (N=370) after small pools had run dry. Alpha ♂ ♂ journeying to water walked steadily, usually following a trail, and paused only momentarily to investigate scents encountered along the way. After drinking they returned directly to their own territories. Immediately they regained their own territory, they spray-urinated several times and commenced grazing. The northern-most territories at Madlozi were 4 to 5 km from permanent water, and for these α ♂ ♂ the return trip to and from water took 3—4 hours. At major waterholes several territories adjoined, so that no α ♂ monopolised the water supply.

The home ranges of cows encompassed some 6—7 ♂-territories. However, based on number of sightings within each territory relative to those of the resident α ♂, most cows spent over 50 % of their time during the wet season within one or the other of two adjacent territories. No individual relationship was evident between a cow and the α ♂ ♂ whose territories were favoured. Seven different cows shared the territory of α ♂ C as their most favoured territory, while in all 26 different cows were seen on two or more occasions within the adjacent territory of α ♂ L. Variations in the average cow population present within each territory (Table 8) seemed related to the relative favourability of the grazing conditions there.

(iii) Beta ♂ ♂. Sighting locations for individual β ♂ ♂ were concentrated within the territories of particular α ♂ ♂ (Fig. 9), so that each territory was co-inhabited by an α ♂ and from 0 to 3 β ♂ ♂ (Table 9). However, β ♂ ♂ wandered outside their home territory limits more frequently than did α ♂ ♂, being en-

Table 8: Mean number of cows present within each territory at Madlozi (wet season conditions only)

Territory	C	L	H – I	X – H	A – X	B	Q
Mean no. of cows	4.2	3.8	2.8	2.7	1.5	1.1	0.6

Fig. 8: Locations of territory boundary blocking actions by α ♂ I and neighbouring α ♂ ♂ L and G

░░░ TERRITORY BOUNDARY
⊣ BLOCKING BY †Ad ♂ I
>   "   "   †Ad ♂s C AND L

N
0   1000
METERS
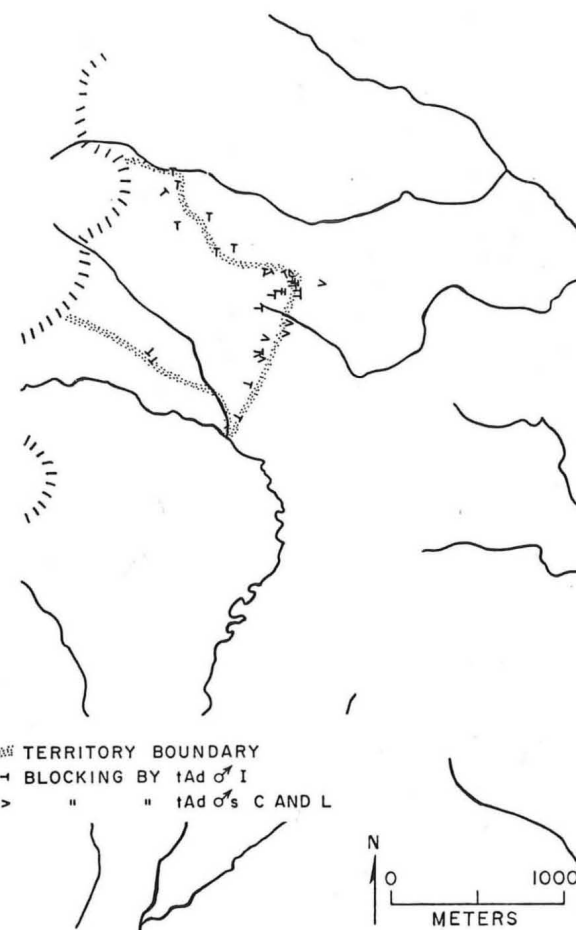
countered elsewhere in 13.0% of all sightings (N= 553) with little seasonal variation. The sole radio-equipped β ♂, a young adult aged about ten years, was recorded within his home-territory in 89 % of all records (N = 253) over a two year period. Excursions seemed to represent exploratory, sallies, and sometimes they brought the β ♂ into confrontation with one of the surrounding α ♂ ♂. Two β ♂ ♂ watched after such an encounter returned directly to their home territories before pausing to graze more than briefly.

Beta ♂ ♂ used the same grazing areas, rest-places and wallows as the α ♂ whose territory they shared, and no avoidance of the α ♂ was evident (see Table 4). After a drinking excursion, β ♂ ♂ usually returned directly to their home territories, but unlike α ♂ ♂ they frequently grazed during the journey back.

(iv) Subadults. For subadult groups home range sizes could be estimated in only a few cases (Table 10) and even these are based on limited numbers of sightings. Subadult ♀♀ seemed to range widely in the manner of cows, even with a sa ♂ as companion; while two sa ♂ pairs each restricted their movements mostly

Table 9: The occurrence of β ♂ ♂ in territories

Study area	No. of territories	0 β ♂	1 β ♂	2 β ♂ ♂	3 β ♂ ♂	total no. of β ♂ ♂
Madlozi , 1966	8	4	4	0	0	4
Madlozi , 1969	11	8	2	1	0	4
Madlozi , 1971	15	10	4	1	0	6
Nqutsheni	6	3	1	1	1	6
Gqoyini	4	2	1	1	0	3
Dengezi	4	3	0	1	0	2
All	48	30	12	5	1	25

Table 10: Home range size of subadults.
Areas measured planimetrically after connecting outlying points

group	observ. period (mo.)	points location		area (km²)		
		radio-telem.	total	core area	home range	annual range
sa♂ + sa♀	18	26	64	5.0	7.0	7.3
sa♂ + sa♀	5	0	32	-	5.0 +	-
sa♂ + sa♂	33	0	39	4.3	4.3	6.1
sa♂ + sa♂	5	0	45	-	2.2	-

to within two α♂ territories. Subadults of both sexes accompanying cows (including young ♂♂ up to about 10 years) moved over the extent of the latter's home range, and such individuals tended to remain in the study area even after separation from the cow. However, there were subadults of both sexes that appeared at Madlozi, which were sighted there regularly over a period of a few days or months, then were not recorded again. Two sa♀♀ eartagged in the study areas were later encountered 15 km and 25 km away respectively. Thus some subadults evidently shifted nomadically from area to area. Settled home ranges were apparently not established by ♀♀ until after the birth of their first calf, and by ♂♂ probably not until they occupied a territory as either a β♂ or α♂.

C. Social dynamics

1. Interactions in direct encounters

A direct encounter was held to have occurred when two rhinos, not associated together in the same group, came sufficiently close together to be judged certainly aware of one another's presence. This occurred at separation distances between

Fig. 10: Nasonasal contact between two subadults. Two cows stand nearby disinterestedly

30 m and 70 m, depending on the orientation and activities of the animals concerned. An encounter may be subdivided into three potential stages: (i) an *initial stage* following awareness perhaps leading to approach or withdrawal; (ii) following an approach, a *confrontation* during which the two individuals face one another at close quarters; (iii) *termination* of the confrontation during which the animals move apart again.

Initial actions may be categorised as follows: (i) *no approach* was made; sometimes no response was shown to the presence of the other; (ii) a *checked approach* was made; one animal started to approach the other, but then turned aside (sometimes because the approached animal immediately withdrew); (iii) one individual *chased after* the other; (iv) *avoidance* was shown; one animal withdrew (slowly or chased), or circled round the other averting a confrontation; (v) one or both individuals *approached to confront*, standing attentively a few metres or less apart; (vi) sometimes one individual terminated such an approach with a sudden rush or *charge*.

Actions during confrontations included the following: (i) one animal stood

Fig. 9: Points of location for four β ♂♂, Madlozi study area, 1 June 1970 — 4 Sept. 1971. Plotted as in Fig. 4

INDIVIDUAL
NO. LOCATION RECORDS   56   112   37   6
TERRITORIAL BOUNDARIES

Fig. 11: Reciprocal horn to horn stare by two neighbouring α ♂♂

Fig. 12: A cow (on the left) advances to clash horns with a β ♂

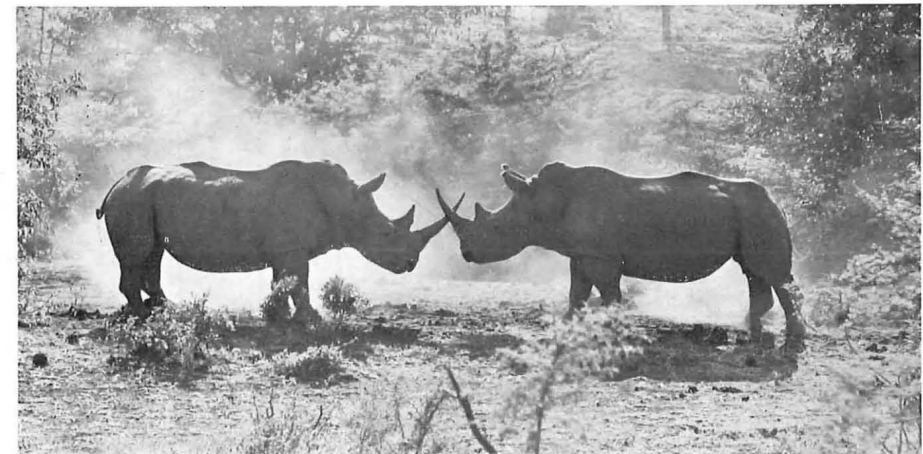facing the other from a few metres away downwind, or both individuals stood relaxed with heads in close *nasonasal contact* (Fig. 10); such actions will be termed generally *olfactory investigations* (they seem analogous to what have been termed "greetings" for example in zebras (KLINGEL 1967); (ii) sometimes following nasonasal contact slow fencing movements with horns pressed together ensued, and sometimes these developed further into playful *horn wrestling* matches; (iii) one animal confronted the other with head raised, and horn in contact or almost in contact with the horn of the other; such action will be termed the *horn to horn stare* (Fig. 11), and is interpreted as an intimidatory gesture emphasizing attributes of smell, body size and confidence (this seems analogous to the classification "superiority display" of WALTHER [1974]); (iv) one animal with lowered head *clashed horns* briefly with the other (Fig. 12); this is interpreted as a "symbolic" attack; (v) one animal *attacked* the other with horn to body blows; a fight ensued when blows were reciprocated by the

Fig. 13: A β ♂ stands giving a snarl display as an α ♂ approaches

other animal; (vi) one animal *retreated* yielding ground before the other during the confrontation; (vii) one animal gave one or more *snorts;* this sound is interpreted as a mild separation-maintaining display; (viii) one animal gave a *snarl* display (Fig. 13); the head was thrust forwards, ears laid back, and mouth opened to let out a loud rasping roar, which sometimes rose in pitch to a shrill shriek; sometimes a snarl was coupled with a few advancing steps, and occasionally an advancing snarl ended in a clash of horns or a horn prodding gesture; a snarl is interpreted as a more powerful separation-maintaining or sometimes distance-increasing display (the term "defensive threat" as used by WALTHER (1974) also seems applicable). (Supporting evidence for the above interpretations has been presented elsewhere [OWEN-SMITH 1973]).

A confrontation was terminated when one or the other of the individuals turned away and withdrew. The remaining individual then either did likewise, or remained standing in the same vicinity.

Table 11 — Responses of alpha ♂ ♂ in encounters.
Figures represent frequencies expressed as proportions of encounters observed proceeding through each stage (Subsample sizes are thus less than total N)

location of α ♂ relative to home territ.	other indiv.	N	initial actions						actions during confrontation							termination
			no approach	checked approach	chases after	avoidance	appr. to confront	propn. charges / approaches	olfact. invest.	horn to horn stare	horn clash	attack	retreat	snort	snarl	initiates moving away
1a. mutual border	neighb. α ♂	25	.28	0	0	0	.72	.83	0	1.00	.41	0	0	0	0	–
1b. within territ.	intrud. α ♂	12	.25	0	.08	0	.67	1.00	0	1.00	.50	.12	0	0	0	.71
1c. neighb. territ.	resid. α ♂	7	.72	0	0	.28	0	–	0	1.00	.80	.20	.80	0	0	.50
1d. distant territ.	resid. α ♂	5	.60	0	0	.40	0	–	0	–	0	0	0	0	1.00	0
2a. within territ.	resid. β ♂	117	.45	.28	.05	0	.22	.29	.03	.97	.31	0	0	0	0	.94
2b. within territ.	intrud. β ♂	41	.19	.08	.15	0	.58	.19	0	1.00	.60	.03	0	0	0	.96
2c. distant territ.	β ♂	5	.80	0	0	.20	0	–	–	–	–	–	–	–	–	–
3a. within territ.	AD ♀	142	.12	.37	0	.01	.52	.07	.95	0	.06	.05	0	0	0	.82
3b. distant territ.	AD ♀	14	.28	.07	0	.43	.22	0	1.00	0	0	0	0	.07	0	1.00
4a. within territ.	sa ♂	69	.30	.41	.12	0	.17	.16	0	.93	.10	.07	0	0	0	1.00
4b. within territ.	sa ♀	20	.15	.35	.10	0	.40	0	.75	0	0	.25	0	0	0	1.00

The type of response shown in an encounter depended not only on the social status of the other individual, but in the case of adult ♂♂ also on the location relative to the home territories of the individuals concerned (Tables 11—14).

Alpha♂-alpha♂ encounters. Most encounters observed between α♂♂ took place at a mutual territory border. However, even such border confrontations

Table 12: Responses of beta ♂♂ in encounters. Figures represent frequencies expressed as proportions of encounters observed proceeding through each stage (Subsample sizes are thus less than total N)

| location of β♂ rel. to home territory | other indiv. | N | initial actions | | | | actions during confront., or approach by other | | | | | termination |
			no approach	checked approach	avoidance	appr. to confront	olfact. invest.	propn. horn wrestl. / nasonasal contacts	horn to horn stare	snort	snarl	initiates moving away
1a. within territ.	resid. α♂	117	.85	0	.15	0	0	.06	0	(.18)	.91	.06
1b. neighb. or distant territ.	resid. α♂	41	.73	0	.27	0	0	0	0	(.07)	1.00	.04
2a. within territ.	resid. β♂	15	.60	.13	0	.27	.87	.33	0	.50	.30	-
2b. within territ.	intrud. β♂	5	.40	.60	0	-	-	0	-	-	-	1.00
2c. distant territ.	β♂	10	.90	0	.10	0	-	0	-	-	-	-
3a. within territ.	AD♀	54	.24	.39	0	.37	.98	0	.02	0	0	-
3b. distant territ.	AD♀	20	.30	.15	.10	.45	1.00	0	0	0	0	-
4a. within territ.	sa♂	32	.34	.28	0	.38	.60	.58	0	(.15)	.15	-
4b. within territ.	sa♀	11	.27	.27	0	.46	1.00	0	0	0	0	-

( ) = minimal estimate.

Table 13: Responses of cows in encounters. Figures represent frequencies expressed as proportions of encounters observed proceeding through each stage

| other indiv. | N | initial actions | | | | actions during confront., or approach by other | | | | |
		noapproach	checked approach	avoidance	appr. to confront	olfact. invest.	propn. horn wrestl. / nasonasal contacts	horn clash	snort	snarl
1. α♂	156	.96	0	.01	.03	.01	0	.03	(.46)	(.56)
2. β♂	74	.96	.01	0	.04	.06	0	.06	(.40)	(.52)
3. AD♀	79	.57	.06	0	.36	.47	.25	.17	(.40)	(.14)
4a. sa♂	56	.77	.16	0	.07	.39	.42	.03	(.43)	(.16)
4b. sa♀	20	.75	.10	0	.15	.43	.50	0	(.43)	0

( ) = minimal estimates.

Table 14: Responses of subadults in encounters. Figures represent frequencies expressed as proportions of encounters observed proceeding through each stage

| | sex | other indiv. | N | initial actions | | | | actions during confront., or appr. by other | | | | |
				no approach	checked approach	avoidance	approach to confront	olfact. invest.	propn. horn wrestl. / naso-nasal contacts	horn clash	snort	snarl
1a.	sa♂	α♂	69	.65	0	.35	0	0	0	0	(.13)	(.36)
1b.	sa♀	α♂	20	.55	0	.45	0	0	0	0	(.06)	(.33)
2a.	sa♂	β♂	32	.69	.16	.12	.03	.50	.58	0	(.19)	(.11)
2b.	sa♀	β♂	11	1.00	0	0	0	.12	0	0	(.50)	(.25)
3a.	sa♂	AD♀	56	.16	.36	.14	.34	.95	.42	0	(.02)	0
3b.	sa♀	AD♀	20	.45	.30	0	.25	1.00	.50	0	0	0
4.	sa♂ or sa♀	sa♂ or sa♀	34	.20	.32	.04	.44	.54	.40	0	(.20)	(.27)

( ) = minimal estimates.

were infrequent. Alpha♂♂ were kept under close observation for a total of about 1500 hours, and in this time only 16 confrontations in the vicinity of a border were witnessed. Hence it is estimated that each α♂ experiences a confrontation with one of his neighbouring α♂♂ on the average once every four days; and, assuming each territory to be surrounded by four neighbouring territories, each neighbouring α♂ is confronted on the average only once every two weeks. Night observations were limited, but since the general activity level at night was similar to that in the day, it is not believed that such encounters occurred much more frequently at night.

Not all border encounters led to a confrontation. In about a quarter of the observed instances, the α♂♂ declined to approach, though at least one and sometimes both were clearly aware of the other. Sometimes one individual horn wiped on the ground on noticing the other. An approach was frequently termi-

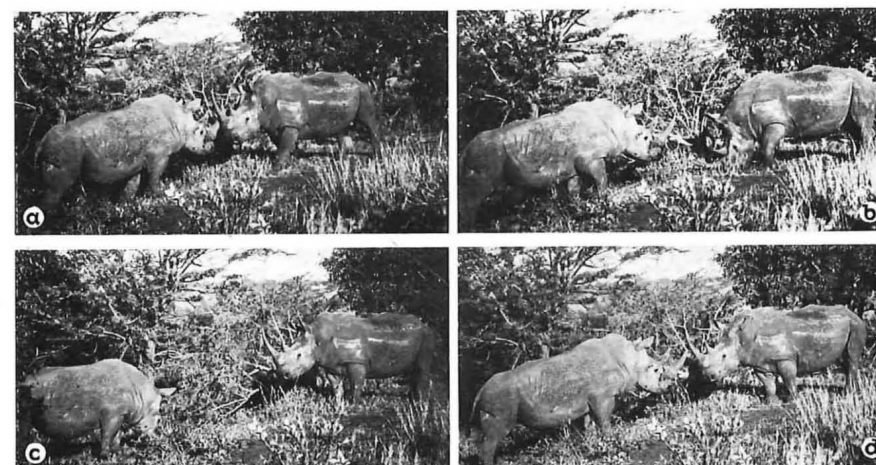*Fig. 14:* A border confrontation between two neighbouring α ♂♂. a. the two ♂♂ confront one another horn to horn; b. one ♂ horn wipes while the other looks on; c. the second ♂ horn wipes while the first watches; d. the two ♂♂ stare horn to horn again
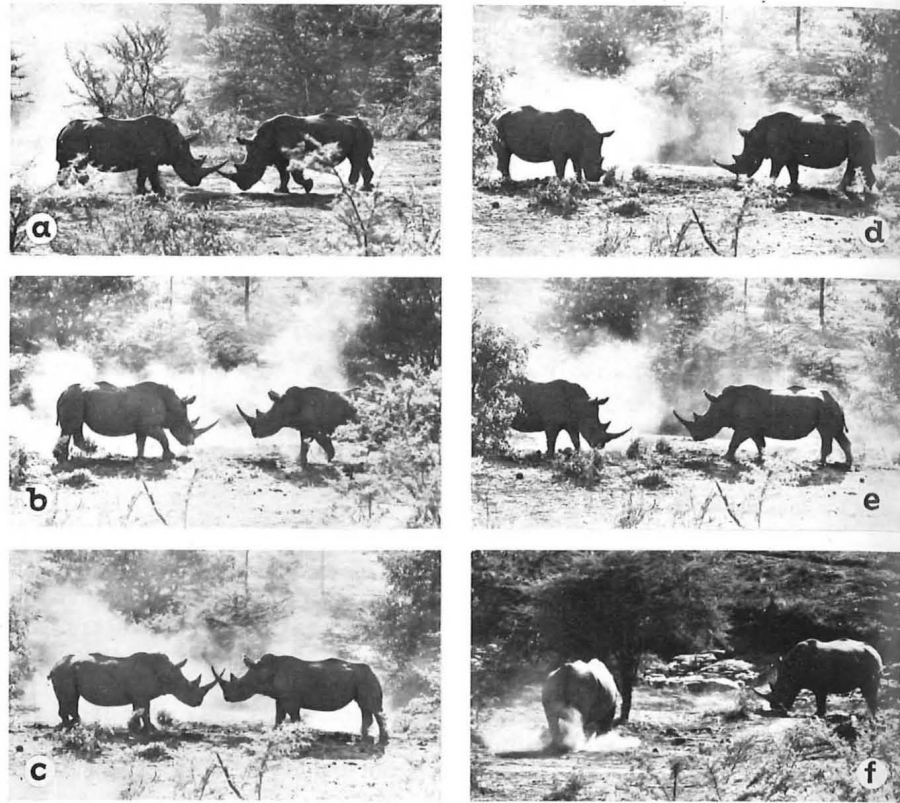
Fig. 15: A confrontation between two neighbouring α ♂ ♂ in which one has intruded into the territory of the other. a. the resident α ♂ (on the right) advances to confront the intruder; b. the intruder backs scraping his hindlegs while the resident advances; c. the two ♂ ♂ stare horn to horn; d. the intruder pauses while the resident is about to horn wipe; e. the intruder resumes backing away; f. the intruder backs away across the watercourse marking the boundary location; the resident ♂ pauses on the bank and scrapes

nated by a charge by one of the α ♂ ♂, but both α ♂ ♂ never charged simultaneously. Three charges ended in a short clash of horns, but usually a charge was checked just before the other α ♂ was met. A second α ♂ faced such a charge standing silently with lowered head.

Border confrontations between neighbouring α ♂ ♂ typically included the following sequence of actions (Fig. 14): (i) reciprocal horn against horn staring; (ii) vigorous horn wiping on the ground; (iii) repetitive advancing to meet horn to horn then retreating to horn wipe over a distance of a few metres. Brief clashes of horns occurred in fewer than half of the observed confrontations. In two instances, one α ♂ simulated grazing while the other looked on. Seven of the observed confrontations were brief, lasting 5 minutes or less, and 8 lasted 7—36 min. One was prolonged for 65 minutes, while another was still in progress after 88 minutes when darkness fell.

Confrontations were terminated when one α ♂, or both α ♂ ♂ simultaneously, turned away side-on, then moved slowly away. One of the α ♂ ♂ scraped and urinated sprays while moving away in 7/12 cases, and in one instance an α ♂ dragged his hindlegs stiffly over the ground while withdrawing.

Encounters in which one α ♂ was intruding into the territory of a neighbour occurred in circumstances in which the trespasser was probably travelling to or from water, except in one instance. The actions of both α ♂ ♂ were generally similar to those described for border confrontations, except that the intruding α ♂ retreated steadily towards his own territory during the course of the confrontation (Fig. 15). Upon reaching his own border the retreating α ♂ scraped and urinated sprays and turned away. The other α ♂ then halted and also moved away.

In one such case an intruding α ♂ did not yield, and there was a fight which had lasted for 35 minutes when darkness fell. There were long periods of slow fencing movements horn pressed against horn, then suddenly one α ♂ attacked the other with repeated blows around the head, shoulders and occasionally the flank, which were fended or reciprocated by the other α ♂. After such a bout, the two α ♂ ♂ stood breathing heavily for several minutes before resuming slow horn fencing. The fight took place near the opposite border of the resident α ♂'s territory to that adjoining the territory of the intruding α ♂, and it seems that retreat towards his own territory by the intruder was impractical in such circumstances. The intruding α ♂ when found the next day still outside his home territory had numerous lacerations and bruises around the head and shoulders and one eye was a bloody mass.

In contrast, an α ♂ intruding on a more distant territory either avoided the resident α ♂, or, if accosted, stood his ground, tail curled, and performed the snarl display repetitively. Two of the observed confrontations lasted less than 5 min, while the third was prolonged for 25 min. The resident α ♂ confronted the intruder horn to horn, advancing then withdrawing a few paces at a time. In all three cases, the resident α ♂ terminated the meeting by turning and moving off. The intruding α ♂ then proceeded back towards his home territory.

Fights perhaps occurred more frequently than direct observations indicate when α ♂ ♂ had to cross other territories on their way to water, since some α ♂ ♂ frequently exhibited fresh gashes around the head during the late dry season. Journeys to water were most commonly made at night and hence were difficult to observe. However, I was able to follow a ♂ during part or all of the journey to or from water on 14 occasions during the day and once at night. These represented a total of 9 trips (one trip = completed journey to and from water) and 45 territories crossed. Only two confrontations with a resident α ♂ took place. Thus, it is estimated that confrontations in such circumstances occur on the average only once every 4.5 trips to water, or once every 22 territory crossings.

Alpha ♂-beta ♂ encounters. If accosted by an α ♂, both resident and intruding β ♂ ♂ stood giving repeated snarls, which rose in pitch to shrieks if the α ♂ made any move suggestive of attack. An α ♂ was more likely to confront an intruding β ♂ than a β ♂ sharing the same home territory (recorded frequencies 0.58 vs 0.22, $\chi^2 = 13.3$, p < 0.005), 50 % of the confrontations with an intruder were prolonged for more than 5 minutes compared with only 6½ % for residents, and horn clashes were more frequent against intruders (0.60 vs 0.31, $\chi^2 = 4.73$, p < 0.05). Alpha ♂ ♂ usually confronted resident β ♂ ♂ for less than a minute, then wandered off. Sometimes an α ♂ walked past a resident β ♂ at close quarters showing no response while the latter made snorts or snarls. More prolonged confrontations with a resident β ♂ occurred in special circumstances: once, when the β ♂ was the deposed former territory holder; and once, after the β ♂ had attempted to court a cow. However, even after the latter provocation the α ♂ did not carry through an attack further than three brief clashes of horns.

Against intruding $\beta\delta\delta$ the horn to horn stare was frequently coupled with advancing then withdrawing a few steps at a time, and sometimes with circling round and readvancing to meet (Fig. 16). In one case an intruding $\beta\delta$ was attacked and chased around for 15 min, and incurred several lacerations. Other $\beta\delta\delta$ were also sometimes noted showing fresh wounds. Again, confrontations were almost always terminated by the $\alpha\delta$, who turned and walked off. In 16/28 cases, the intruding $\beta\delta$ thereupon departed from the territory; in 5/28 cases, he moved away from the vicinity of the confrontation, but not from the territory; in 7/28 cases, he remained in the same place. In the latter instances it is possible that the intruding $\beta\delta$ might have left the territory some time later after I had departed. Beta $\delta\delta$ retreating at the approach of an $\alpha\delta$ were young adults all.

Of the five instances in which a wandering $\alpha\delta$ encountered a $\beta\delta$, three took place at drinking pools. In these circumstances the $\alpha\delta$ looked towards the $\beta\delta$ without approaching, making either snorts or snarls, while the $\beta\delta$ responded with snorts. In a fourth encounter, the $\alpha\delta$ stared at the $\beta\delta$, then hastened back towards his own territory which lay only 100 m away. In the fifth case, the $\alpha\delta$ passed by the $\beta\delta$ at 75 m range. Neither responded to the other, but after the $\alpha\delta$ had passed the $\beta\delta$ followed its scent tracks a short way.
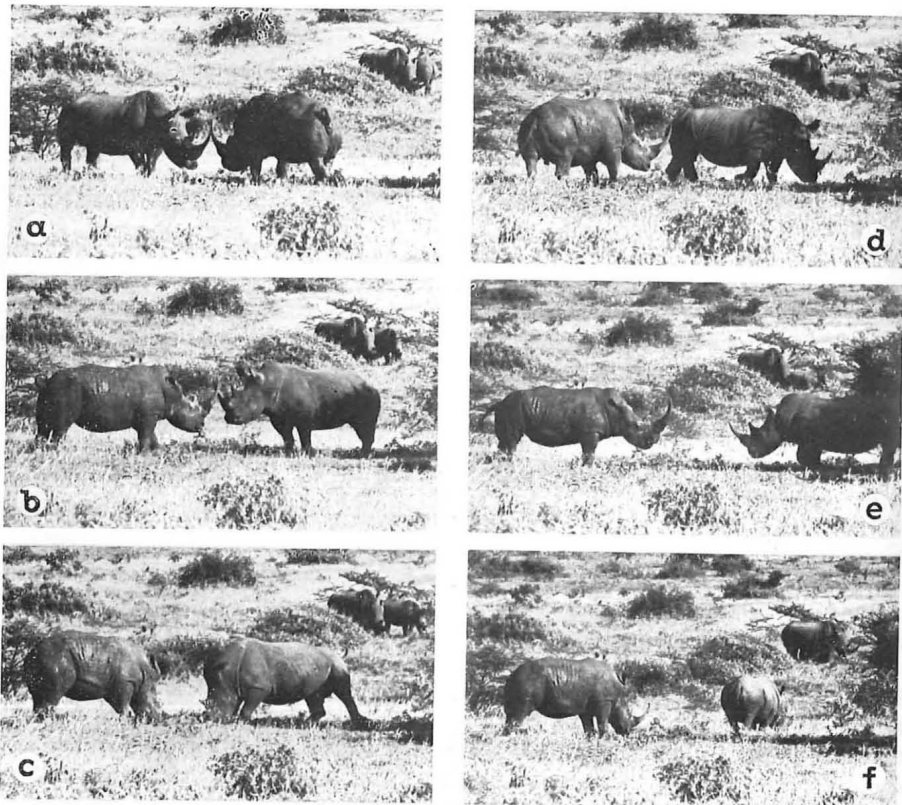

Fig. 16: A confrontation between a resident $\alpha\;\delta$ and an intruding $\beta\;\delta$. a. the resident $\alpha\;\delta$ (on the left) stares at the $\beta\;\delta$ horn to horn; the $\beta\;\delta$ responds with a snarl display; b. the $\alpha\;\delta$ confronts the $\beta\;\delta$ from a different direction; the $\beta\;\delta$ snarls; c. the $\alpha\;\delta$ springs forwards to clash horns; the $\beta\;\delta$ defends; d. the $\alpha\;\delta$ circles round ... e. and advances to confront the $\beta\;\delta$ again; the $\beta\;\delta$ snarls; f. the $\alpha\;\delta$ wanders away towards a cow and calf standing in the background; the $\beta\;\delta$ relaxes

Fig. 17: One-sided olfactory investigation by an $\alpha\delta$ (on the left); the cow gives a snarl display

Only one supplanting interaction was recorded. A resident $\beta\delta$ moved away from a shady rest-place as the $\alpha\delta$ approached, and the $\alpha\delta$ lay down there while the $\beta\delta$ sought out another site 40 m away. However, in another observation in similar circumstances the $\beta\delta$ lay giving snorts and snarls when the $\alpha\delta$ approached, and the $\alpha\delta$ settled at another tree 12 m away.

Beta δ-beta δ encounters. Beta $\delta\delta$ that were coinhabitants of the same territory usually paid little attention to one another. Sometimes the upwind $\beta\delta$ made snorts or snarls when the other moved close by, perhaps due to inability to identify its status. Three approaches led to reciprocal nasonasal contact, and one of these developed into a playful horn wrestling contest; both $\beta\delta\delta$ concerned were young adults.

In two instances, a resident $\beta\delta$ advanced towards an intruding $\beta\delta$, but veered away when the latter stood defensively with snarls. In one encounter which took place near the border between their respective home territories, both $\beta\delta\delta$ stood tensely 10 m apart for 33 min. At waterholes, one or both directed snorts or snarls towards the other.

Alpha δ-cow encounters. Resident $\alpha\delta\delta$ commonly approached cows to stand a few metres away usually downwind staring intently at the cow (Fig. 17). After perhaps a minute, the $\alpha\delta$ then usually moved away. Sometimes he stayed, commencing grazing or some other activity near the cow. Approaches were commonly accompanied by a hiccing sound used also in courtship. Cows responded to approaches by turning to face the $\alpha\delta$ with snorts or snarls. In five cases a cow advanced on an $\alpha\delta$ with a snarl causing the $\alpha\delta$ to give way, once with a clash of horns initiated by the cow. Four cases were observed in which an $\alpha\delta$ suddenly attacked a cow, but all attacks were brief and no obvious damage was inflicted. There was suggestive evidence that attacks, and also the occasional charges directed by $\alpha\delta\delta$ towards cows, were due to misidentification.

Alpha $\delta\delta$ outside their home territories usually circled round avoiding meetings with cows. Once at a waterhole an $\alpha\delta$ snorted at the approach of a cow; the cow then advanced with a snarl to clash horns.

Beta δ-cow encounters. Resident $\beta\delta\delta$ approached cows, but did so less frequently than resident $\alpha\delta\delta$ (0.77 vs 0.88, $\chi^2 = 4.44$, $p < 0.05$), and their movements were more hesitant. The behaviour of wandering $\beta\delta\delta$ was similar. Cows responded to such approaches as they did to $\alpha\delta\delta$. However, two reciprocated nasonasal contacts were observed.

Cow - cow encounters. Cows commonly showed little response to one another. Sometimes an approach was made leading to nasonasal contact, and a quarter of these developed into playful horn wrestling. However, on other occasions one cow responded to the approach of another with a snort or snarl. Horn clashes were observed in six instances. Three of these occurred at drinking pools, and in another two cases the cow initiating the clash was accompanied by a small infant.

Encounters involving subadults. Alpha ♂ ♂ usually approached sa♂ ♂, but confrontations were brief when they occurred. Except when accompanying a cow, younger subadults tended to retreat if approached by an α♂, and in a few cases the α♂ chased after a short way. One sudden attack on a four-year old sa♂ and two on sa♀♀ were witnessed but no damage was evident. However, there are reports of sa♂ ♂ found dead with horn wounds.

Subadult ♂ ♂ also sometimes retreated if approached by a β♂. However nasonasal contacts sometimes occurred and frequently developed into playful horn wrestling matches.

Subadults of both sexes commonly approached cows and other subadults, though occasionally such approaches were checked by snorts from the other individual. Approaches frequently developed into nasonasal contacts and horn wrestling. Similar horn wrestling was also a common feature of meetings between calves and between calves and subadults.

Summary and comparisons. The usual response of an α♂ within his home territory on encountering another rhino was to approach. If the other rhino was a ♀, the α♂ engaged in a one-sided olfactory investigation. If it was a β♂ sharing the same territory, then there was commonly a brief horn to horn confrontation. If it was another α♂ or an intruding β♂, then there was a more prolonged horn to horn confrontation. Attacking gestures were mostly limited to brief horn clashes, and it was almost invariably the resident α♂ that moved away first. Fights were rare.

On a neighbouring territory, an α♂ maintained the silent horn to horn stare but retreated. On a more distant territory, he exhibited the behaviour of a β♂.

Cows, β♂ ♂ and older subadults responded to an approach by an α♂ with separation maintaining displays. Beta ♂ ♂ continued snarling repetitively as long as the α♂ remained confronting. Only younger subadults commonly retreated.

Cows and subadults either showed little response to one another or approached for reciprocal olfactory investigation. Sometimes playful wrestling developed, subadults (and also calves) being the more active in initiating such action, and sa♂ ♂ also occasionally engaged in playful wrestling with β♂ ♂.

2. Indirect encounters mediated by auditory or olfactory signals

Though snarls might be audible 1 km or more away, no rhino was ever seen to respond to such sounds at a distance.

The only scent glands reported in the white rhinoceros are preputial glands (CAVE 1966); pedal scent glands are apparently restricted to the Asian genus *Rhinoceros* (CAVE 1962). However, the olfactory stimuli emanating from both dung and urine can serve as social signals, not only providing evidence of the recent presence of another conspecific in the area, but also potentially indicating its sex and perhaps even individual identity (EISENBERG and KLEIMAN 1972).

Rhinos tend to defecate where other rhino dung is already present, so that large dungheaps are a feature of rhino habitat (Fig. 18). Dungheaps were con-

Fig. 18: A large white rhino dungheap. In the foreground are the scattered dung piles of cows or β ♂ ♂; in the background is a hollowed out dung accumulation produced by the kicking actions of an α ♂

centrated particularly around resting and drinking areas and beside trails, and were used by rhinos of all social categories. However, α♂ ♂ restricted defecation almost exclusively to dungheaps, and usually orientated their hindquarters specifically to the centre of the dungheap; while β♂ ♂ and cows sometimes defecated away from a dungheap, or merely in the general vicinity of the dungheap rather than on the central pile (Table 15). Also, α♂ ♂ invariably made powerful kicking movements before and after defecation, so that their dung was broken up and scattered over the heap. Beta ♂ ♂ and cows sometimes made a few kicking motions before and after defecation (Table 15), but except in a few instances these were without power and did not disturb the dung pile.

Dungheaps were scattered throughout the extent of a ♂-territory; 30 dungheaps of varying size were counted within the territory of one α♂ (Fig. 19). However, present along borders were certain large, well-hollowed out dungheaps attesting to frequent visitations by an α♂. Daily monitoring of such dungheaps for signs of kicking revealed that they were marked by an α♂ on the average every second day.

Alpha ♂ ♂ journeying to water sometimes defecated at dungheaps in other territories, and made the usual kicking movements.

Rhinos of all social castes frequently sniffed carefully at dungheaps and also at scattered dung piles encountered away from dungheaps. Alpha ♂ ♂ in particular sometimes spent several minutes sniffing at a dungheap before defecating there. In nine observed instances, an α♂ dug his anterior horn deeply

Table 15: Defecation patterns

	location		preceding kicks			following kicks		
	on dung-heap	centrally located	instances	mean number +	range	instances	mean number +	range
α ♂♂	27 / 29	19 / 22	69 / 69	7.2	1 - 28	99 / 99	9.7	2 - 19
β ♂♂	10 / 19	5 / 9	5 / 39	3.4	0 - 11	22 / 47	3.8	0 - 10
AD ♀♀	28 / 54	3 / 13	0 / 91	-	-	10 / 91	3.2	0 - 25*

* Exceptional instance excluded in calculating average.
+ Including only instances when kicks were given.